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The unnatural grouping of *Deuterodiscoelius* Dalla Torre, 1904, and *Pachycoelius* Giordani Soika, 1969 (Hymenoptera, Vespidae), and a remarkable new species

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ABSTRACT

Deuterodiscoelius Dalla Torre and *Pachycoelius* Giordani Soika are two small genera of Australian vespid wasps. While the first came from the splitting of *Discoelius*, the latter was created to accommodate species with a few distinct traits, some of which were not observable due to the absence of male specimens of two out of the three species designated to the genus. This already blurry delimitation of the genera was heightened when specimens of an unknown species presented a combination of characters from both genera. Hence, to properly assign this species to a genus, a phylogenetic study based on morphology was carried out before the species description. The analysis recovered both genera as unnatural, resulting in the synonymy of *Pachycoelius* under *Deuterodiscoelius*, and the new species, namely, *Deuterodiscoelius delator* Lopes and Carpenter, new species, was subsequently described.

INTRODUCTION

Deuterodiscoelius Dalla Torre, 1904, is a genus of zethine potter wasps comprising six extant species, all exclusive to the Australian Region. The taxonomic history of this group (fig. 1) is traced back to *Discoelius* Latreille, 1809, when de Saussure (1852) partitioned the genus

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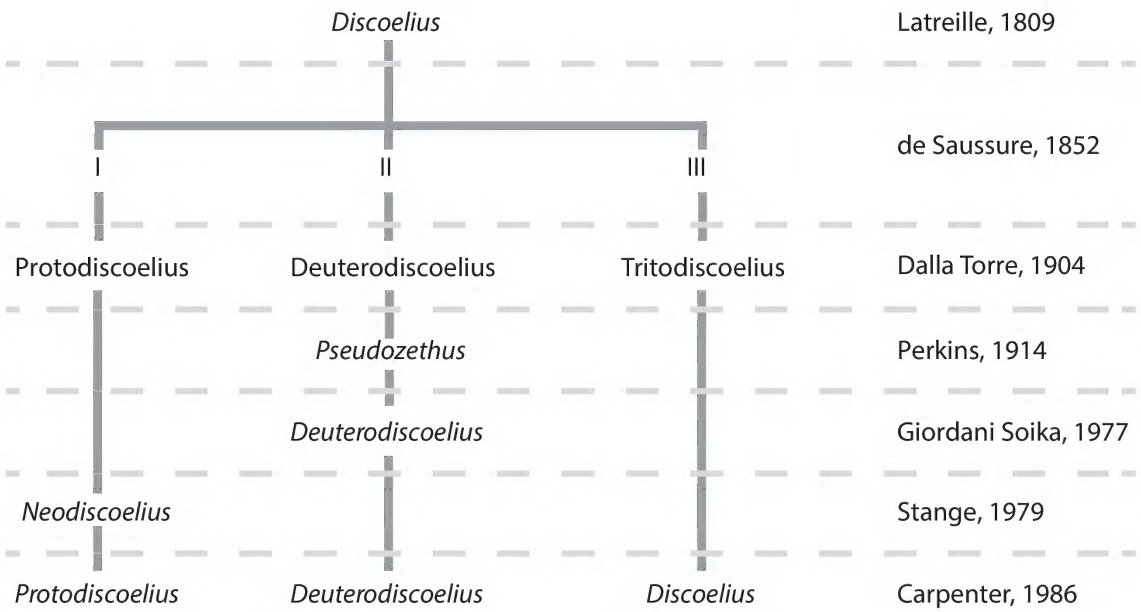

FIGURE 1. History of taxonomic divisions and changes of *Discoelius* Latreille.

into three divisions following both morphological and geographical distribution of its representatives. Each division was assigned a roman numeral: Division I held neotropical species, Division II, Australian, and Division III, palearctic species.

Dalla Torre (1904) kept the divisions proposed by de Saussure, agreeing with both criteria for their separation, but provided names for these divisions. Thus, the neotropical species division was established as *Protodiscoelius*, the Australian, *Deuterodiscoelius*, and the Palearctic, *Tritodiscoelius*. These names were ignored when Perkins (1914) created the genus *Pseudozethus* for a single species, *P. australensis*. Giordani Soika (1969) revised the genus, but only later (Giordani Soika, 1977), after learning from van der Vecht that the group had a senior name, did he synonymize *Pseudozethus* under *Deuterodiscoelius*. Two species were then properly assigned to the new name combination while the remainder were assigned to it only recently (Carpenter and Brown, 2021a).

A similar path was followed when Stange (1979) described *Neodiscoelius*, only to be later synonymized under *Protodiscoelius* by Carpenter (1986). Without these divisions, *Discoelius* is now comprised of only Palearctic and Oriental species and the division *Tritodiscoelius* is unnecessary.

Pachycoelius Giordani Soika, 1969, was created encompassing only three Australian species. Its diagnostic characters included a short propodeal valvula (fig. 2A), long maxillary palpi (fig. 2B) and males with the last flagellomere reduced (fig. 2C). These traits contrast with those of *Deuterodiscoelius*: an elongated propodeal valvula (fig. 2D) and shorter palpi (fig. 2E), and males with a well-developed last flagellomere (fig. 2F). However, at the time, the male of *Pachycoleius* was known only for the type species and the placements of the other two species were uncertain, with Giordani Soika himself raising the possibility that they could actually belong to *Deuterodiscoelius*.

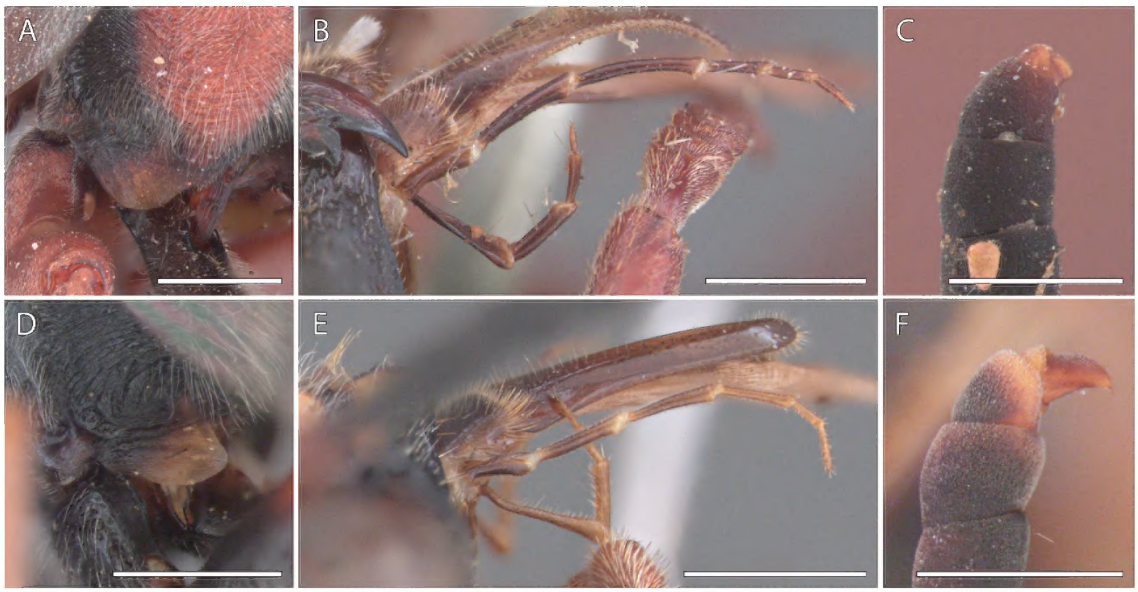

FIGURE 2. Diagnostic characters of *Pachycoelius* Giordani Soika (A–C), and *Deuterodiscoelius* Dalla Torre (D–F). A, D. Propodeal valvula, lateral oblique view. B, E. Maxillary (above) and labial (below) palpi. C, F. Apex of male flagellum. Scales: 1 mm.

The unclear definition of these two genera became evident even before investigating the taxonomic history, when females of an undescribed species were examined. The examined specimens presented short palpi, even shorter than those typical of *Deuterodiscoelius*, and a short propodeal valvula, typical of *Pachycoelius*. This combination of characters made it impossible to assign the new species to one of these genera. Nomenclatural acts should be done parsimoniously, avoiding unnecessary accumulated changes that might derive from a species description without the knowledge of its true generic identity. Therefore, in this case, a study on genus-level taxonomy should precede the description of the species.

Thus, the aim of this study was to closely examine species of *Deuterodiscoelius* and *Pachycoelius* in order to verify through a cladistic analysis that these genera are indeed natural phylogenetic units regarding each other, and then to describe the yet unknown species.

MATERIALS AND METHODS

The following institutions collaborated with the study by providing specimens: AMNH, American Museum of Natural History, New York; AMS, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; MSNVE, Museo Civico do Storia Naturale di Venezia Giancarlo Ligabue, Venice; ZMUC, Zoological Museum, University of Copenhagen, Copenhagen.

Specimens were observed with the aid of a MZ16 Leica stereoscope. Male genitalia were extracted from relaxed specimens and were then immersed in potassium hydroxide 10% solution for up to 24 hours, followed by neutralization in 10% acetic acid, and were then rinsed and finally stored in glycerin.

For the phylogenetic analysis *Deuterodiscoelius* and *Pachycoelius* species were all used as the ingroup, examining specimens in hand, except for *P. mediocris*, which was examined through pictures on the ZMUC website (ZMUC, 2021) alongside its original description. Since not all its structures were observable or described, *P. mediocris* was eliminated from the phylogenetic analysis, as its large number of missing characters would jeopardize the study. All examined material is provided in Supplementary Material 1 (deposited in the Open Science Framework, DOI 10.17605/OSF.IO/qhs8n).

For outgroups, *Discoelius zonalis* (Panzer, 1801) (deposited in AMNH, ZMUC), *Australozethus tasmanienesis* Giordani Soika, 1969 (ANIC, ANM), *Elimus australis* de Saussure, 1852 (ANM), *Zethus* (*Ischnocoelia*) *exiguus* (Borsato, 2003) (AMNH), *Macrocalymma smithianum* Perkins, 1908 (ANM, ANIC), *Paramischocyttarus buyssoni* Gribodo. 1896 (AMNH) and *Protodiscoelius merula* (Haliday, 1836) (AMNH, ZMUC) were used. The last was used for rooting the tree.

The character matrix was built in Winclada (Nixon, 2015). Characters were equally weighted and unordered. Tree search was carried in the TNT software (Goloboff et al., 2008) with the branch and bound algorithm through the implicit enumeration command. Symmetric resampling (Goloboff et al., 2003) was done with 1000 replications of traditional searches for calculating support, provided as support minus contradiction group (GC) value.

Trees were plotted in Winclada and edited on Adobe Illustrator. Pictures were captured in the Leica Application Suite X with a Flexacam C1 camera attached to a Leica M205C stereomicroscope and stacked in Helicon Focus. Image plates were built in Adobe Photoshop.

The external morphology terminology follows mainly Carpenter and Garcete-Barrett (2002), Bohart and Stange (1965) and Lopes and Noll (2014) for sculpture description and Bitsch (2012) for genitalia morphology. Herein, the following terms are abbreviated: F, flagellomere, S, sternum, and T, tergum.

RESULTS AND DISCUSSION

Character List

A total of 48 characters were circumscribed, seven being from the head, 21 from the mesosoma, 12 from the metasoma, and 12 from the male genitalia. The matrix resulting from assigning character states to each terminal can be found in the Supplementary Material 2 (deposited in the Open Science Framework, DOI 10.17605/OSF.IO/ qhs8n).

Head

0. Longitudinal interantennal carina: 0, absent; 1, present.
1. Transversal interantennal carina: 0, absent; 1, present.
2. Clypeus, median tooth 0, absent; 1, present.
3. Clypeus, apex: 0, not delimited; 1, delimited by a thin, usually smooth margin that contrasts with the sculpture on the remaining surface of the clypeus.
4. Maxillary palpus: 0, short, third palpomere clearly shorter than the combined three apical articles; 1, long, third palpomere subequal or longer than the combined three apical articles.
5. First labial palpomere: 0, straight; 1, recurved.
6. Occipital carina, dorsal portion: 0, continuous; 1, medially interrupted.

7. Occipital carina, ventral portion: 0, absent; 1, present as small ramification; 2, complete.

Mesosoma

8. Pronotal carina, aspect: 0, short; 1, lamellar.
9. Pronotal carina, median notch: 0, absent; 1, weak; 2, deep.
10. Humeral angles: 0, regular; 1, projected.
11. Pretegular carina: 0, absent; 1, incomplete.
12. Mesoscutum, medial carina: 0, absent; 1, present.
13. Tegula, widest at: 0, middle; 1, posterior half.
14. Mesepimeron: 0, beveled; 1, tumescent.
15. Metanotum, projections: 0, absent; 1, present.
16. Metanotum, projections, aspect 0, rounded; 1, sharp.
17. Fourth foretarsomere, apical spines: 0, absent; 1, present.
18. Hind coxa, carina: 0, complete; 1, incomplete.
19. Propodeum, lateral carina, height: 0, regular throughout; 1, raised on propodeal angle.
20. Propodeal angle, dorsal view: 0, regularly convex; 1, angled.
21. Propodeal canal, pit: 0, absent; 1, present.
22. Propodeum, apical rim: 0, absent; 1, present.
23. Propodeal orifice: 0, short; 1, elongated.
24. Propodeum, apical lamella: 0, absent; 1, present.
25. Propodeal valvula: 0, short; 1, projected posteriorly.

Metasoma

26. T1, stem: 0, short, shorter than one third of total sclerite length; 1, long, longer than one third of total sclerite length.
27. T1, longitudinal dorsal carina: 0, absent; 1, present.
28. T1, dorsal convexity: 0, regular; 1, angular.
29. T1, expansion width: 0, wide, over twice as wide as stem; 1, narrow, less than twice as wide as stem.
30. T1, expansion length: 0, short, at most as long as wide; 1, medium (at most three times longer than wide); 2, long (over three times longer than wide).
31. T1, vertical constriction: 0, gradual; 1, abrupt.
32. T1, apical horizontal constriction: 0, absent; 1, weak, apex nearly as narrow as maximum width; 2, strong, apex clearly narrower.
33. T2, apical lamella: 0, absent; 1, present.
34. T2, apical lamella length: 0, normal; 1, reduced.
35. S2, triangular smooth at base: 0, absent; 1, present.
36. T3, lamella: 0, absent; 1, present.

Male genitalia

37. Gonocoxite: 0, narrow; 1, wide.
38. Gonocoxite, apex: 0, rounded; 1, truncate.
39. Aedeagus, basal plate: 0, normal; 1, reduced.
40. Aedeagus, basal plate, length: 0, longer than wide; 1, at most as long as wide.
41. Aedeagus, basal plate, hood—when vey tip is strongly curved ventrally: 0, absent; 1, present.
42. Aedeagus, apodemes: 0, rounded; 1, flat.
43. Aedeagus, ventral lobe, size: 0, small, not passing ventralmost reach of apodeme; 1, large, reaching or passing ventralmost reach of apodeme.

44. Aedeagus, apex alignment: 0, ventrally curved; 1, dorsally curved.
45. Aedeagus, apex of head: 0, closed; 1, open.
46. Digitus, basal projection: 0, absent; 1, present.
47. Cuspis, basiventral projection: 0, absent; 1, present.

Cladistic Analysis and Genus-level Taxonomy

The analysis obtained a single tree (fig. 3). This tree supports Giordani Soika's (1969) claim of *Pachycoelius* being closely related to *Deuterodiscoelius*, because their representatives are all included in an exclusive clade with high support values (fig. 4). This group is supported by five synapomorphies; two of them homoplastic: presence of the interantennal transverse carina (fig. 5A) and presence of a median clypeal tooth (fig. 5B); and three of them unique synapomorphies: pronotal carina interrupted by a strong median notch (fig. 5C), projected humeri (fig. 5C), and mesoscutum with an anterior median carina (fig. 5C).

However, this close relationship does not uphold the current classification. Both genera were recovered as unnatural groups, *Deuterodiscoelius* as paraphyletic and *Pachycoelius* as polyphyletic. While *P. carinatus* is sister group to all other species in the clade, *Deuterodiscoelius* species are distributed in two clades. The first clade is comprised of *D. confusus* and *D. verreauxi*, and is supported by two unique synapomorphies: the strongly angulate metanotal projections (fig. 5D) and the basal plate of the aedeagus hood shaped (fig. 5E). The second clade, where *P. brevicornis* is more closely related to the remaining *Deuterodiscoelius,* is also supported by two synapomorphies: one homoplastic (the absence of an apical lamella on T3; fig. 5G) and one unique (apex of aedeagus open; fig. 5F). The new species stands as sister group to this clade.

Two of the diagnostic traits that separated *Pachycoelius* and *Deuterodiscoelius* reveal themselves as probable convergences. The elongated palpi appears as autapomorphies for *P. carinatus* and *P. brevicornis*. Meanwhile, the propodeal valvula presents ambiguous optimization for the entire clade. The reduced last flagellomere of the male should be considered a specific trait of *P. brevicornis*, as the male of *P. carinatus* was examined and presented a well-developed last flagellomere (the male of *P. mediocris* is still unknown).

Due to this configuration, wherein the genera do not represent natural groups, *Pachycoelius* is here proposed as a new junior synonym of *Deuterodiscoelius*.

Deuterodiscoelius Dalla Torre, 1904

Discoelius (p.p., Division II) de Saussure, 1852: 24 (division of *Discoelius*).

Deuterodiscoelius Dalla Torre, 1904: 18 (name for Division II of *Discoelius*). Giordani Soika, 1977: 109 (senior syn. of *Pseudozethus*). Carpenter, 1986: 19 (cat.). Vecht and Carpenter, 1990: 19 (cat.). Naumann et al., 1991: 979. (characters, distribution, species number), 981 (figure). Carpenter and Brown, 2021a: 10 (cat.); 2021b: 88 (key).

TYPE SPECIES: *Discoelius verreauxii* de Saussure, 1852.

Pseudozethus Perkins, 1914: 622 (genus). Bohart and Stange, 1965: 11 (key to genus). Giordani Soika, 1969: 26 (key for genus), 39 (revision, key for species); 1977: 109 (junior syn. of *Deuterodiscoe-*

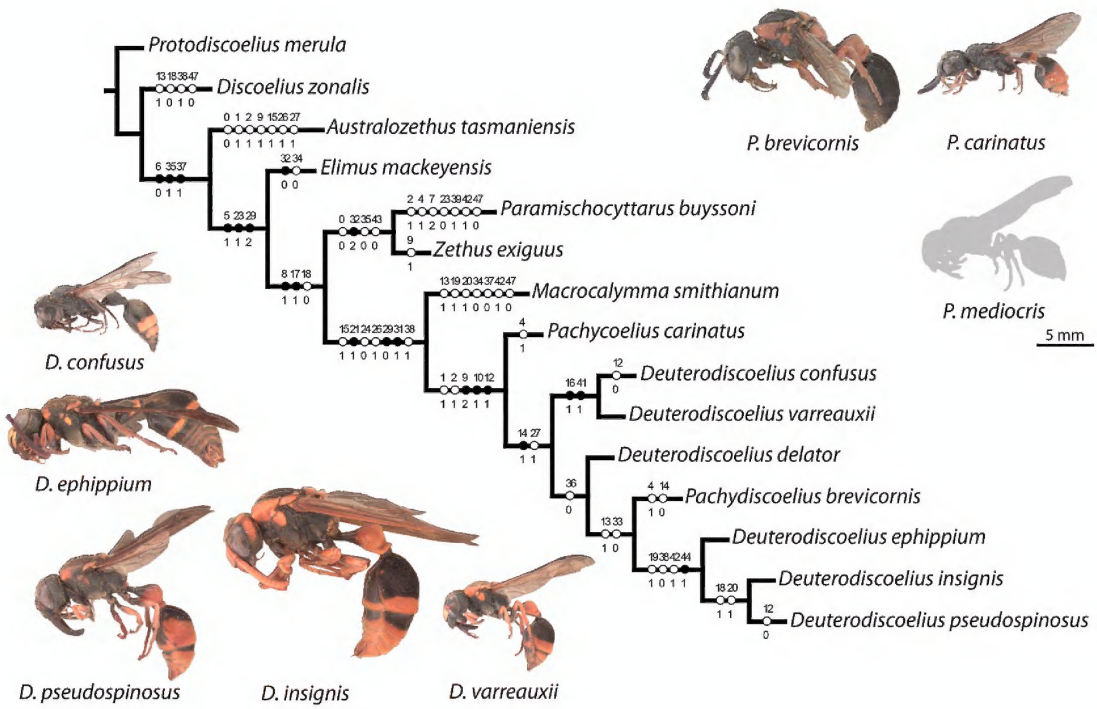

FIGURE 3. Phylogenetic tree resulting from the analysis of *Deuterodiscoelius* and *Pachycoelius*. Black circles represent unique synapomorphies and white circles, homoplasies. Numbers above indicate character number and below, character state.

lius). Stange, 1979: 735 (key to genus), 738 (species number, distribution). Vecht and Carpenter, 1990: 51 (cat.).

TYPE SPECIES: *Pseudozethus australensis* Perkins, 1914 [= *Discoelius verreauxii* de Saussure, 1852].

Pachycoelius Giordani Soika, 1969: 54 (genus). Stange, 1979: 735 (key), 738 (species number, distribution). Vecht and Carpenter, 1990: 39 (cat.). Cardale, 1985: 181–182 (cat.). Naumann et al., 1991: 979 (characters, distribution, species number). Carpenter and Brown, 2021a: 15 (cat.); 2021b: 88 (key). New synonymy.

TYPE SPECIES: *Pachycoelius brevicornis* Giordani Soika, 1969.

INCLUDED SPECIES: *D. brevicornis* (Giordani Soika), *D. carinatus* (Meade-Waldo), *D. confusus* (Giordani Soika), *D. delator* Lopes and Carpenter, *D. ephippium* (de Saussure), *D. insignis* (de Saussure), *D. mediocris* (Giordani Soika), *D. pseudospinosus* (Giordani Soika), *D. verreauxii* (de Saussure).

DIAGNOSIS: Clypeus usually with a median tooth. Maxillary palpi of variable length. Pronotum with dorsal carina lamellar and projected humeri, medially interrupted by a deep notch. Propodeal valvula variable.

OBSERVATIONS: Giordadni Soika (1969) affirmed there is close relationship between *Deuterodiscoelius* and *Zethus*, the main difference being the absence of the apical lamella on T2. However, a thorough examination reveals existence of the structure in most species, but in a

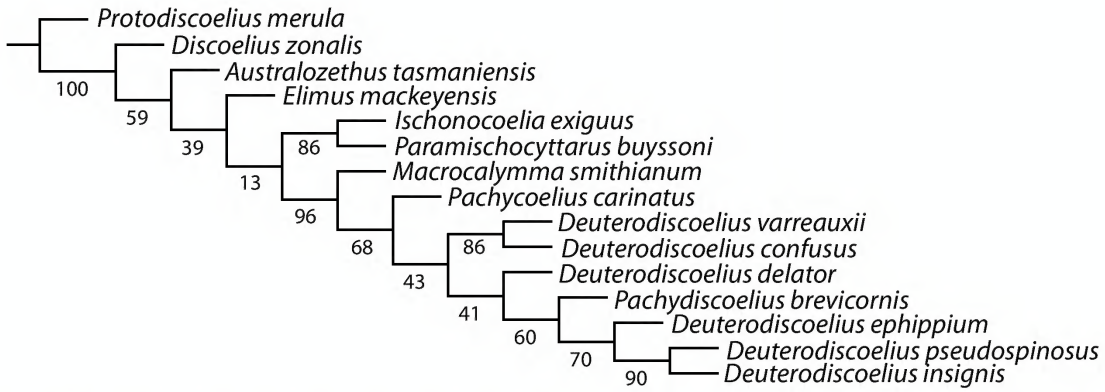

FIGURE 4. Phylogeny showing symmetric resampling support values of contradictory groups for each clade.

reduced state, as the structure is only truly absent in *D. insignis* and *D. pseudospinosus*. Still, we find *Macrocalymma* as sister group to *Deuterodiscoelius*, confirming Giordani Soika's (1969) claim of unarguable affinity between the genera.

The structure of the propodeal valvula is a character usually constant among eumenine genera and commonly used as diagnostic to separate genera in identification keys (Buck et al., 2008; Carpenter and Garcete-Barrett, 2002; Giordani Soika, 1969; Tan et al., 2020). The projected trait of the structure appears in *Zethus, Paramischocyttarus, Macrocalymma* and *Deuterodiscoelius,* but the great variation among lineages of the latter renders the optimization ambiguous. The analysis allows three scenarios (fig. 6): the projected state could be plesiomorphic with independent origins to the not-projected trait in former *Pachycoelius* species and *D. delator*; the non-projected state originated once for *D. carinatus* and once in the closest common ancestor of *D. delator* and *D. brevicornis* with a reversion in the clade of *D. insignis, D. ephippium* and *D. pseudospinosus;* or the not-projected state could be a synapomorphy for the clade, with reversals in the two clades of *Deuterodiscoelius* s. str. Nevertheless, the fact that there is such variability within a genus with only a few species is an exception in the subfamily.

Species-level Taxonomy

Due to the proposed generic synonymy, species previously assigned to *Pachycoelius* must be formally transferred to *Deuterodiscoelius* through new combinations and the new species (fig. 7) is described.

Deuterodiscoelius brevicornis (Giordani Soika, 1969), new combination.
Pachycoelius brevicornis Giordani Soika, 1969: 55 (key, male). Carpenter and Brown, 2021a: 15 (cat.).

TYPE: Holotype, male – Australia, Dudiniu (MSNVE).

Deuterodiscoelius carinatus (Meade-Waldo, 1910), new combination.
Discoelius carinatus Meade-Waldo, 1910: 38 (female). Bequaert, 1928: 158 (cat.). Yasumatsu, 1934: 14 (cat.). Carpenter and Brown, 2021a: 15 (cat.).

TYPE: Holotype, female – Australia, Victoria (NHM).
Pachycoelius carinatus Giordani Soika, 1969: 55 (key), 58 (female, n. comb. for *Discoelius carinatus*).

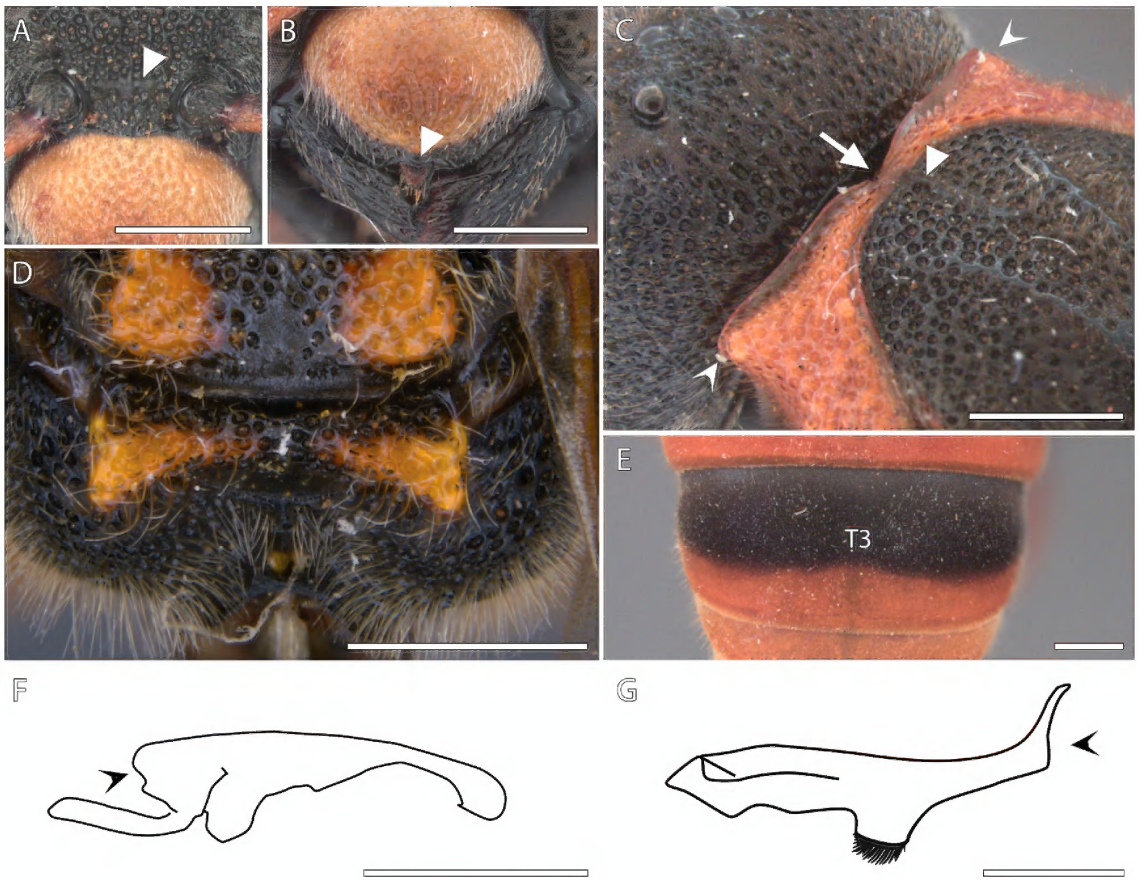

FIGURE 5. Synapomorphies supporting relationships of *Deuterodiscoelius* species. A. Frons; triangle indicates interantennal carina. B. Clypeus, frontal view; triangle indicates median tooth. C. Pronotum and mesoscutum, oblique view; arrow points to notch on pronotal carina; arrowheads show projected humeri; triangle indicates median carina. D. Metanotum of *D. varreauxii*, dorsal view. E. Third metasomal tergum (T3), dorsal view. F. Aedeagus of *D. confusus,* lateral view; arrowhead shows hoodlike basal plate. G. Aedeagus of *D. pseudospinosus,* lateral view arrowhead shows open tip of head. Scales: 1 mm.

Deuterodiscoelius mediocris (Giordani Soika, 1969), new combination.

Pachycoelius mediocris Giordani Soika, 1969: 55 (key), 60 (female). Carpenter and Brown, 2021a: 15 (cat.).

TYPE: Holotype, female – Australia (ZMUC).

Deuterodiscoelius delator Lopes and Carpenter, new species

Diagnosis: The maxillary palpi shorter than the labial palpi (fig. 7C) is unique in the genus, as is the combination of a short palpi with a short propodeal valvula (fig. 7D).

Description: Female.

Coloration: Black, with the following yellow markings: subdorsal transversal band on clypeus; anterior band on pronotum behind the base of dorsal carina and interrupted medially;

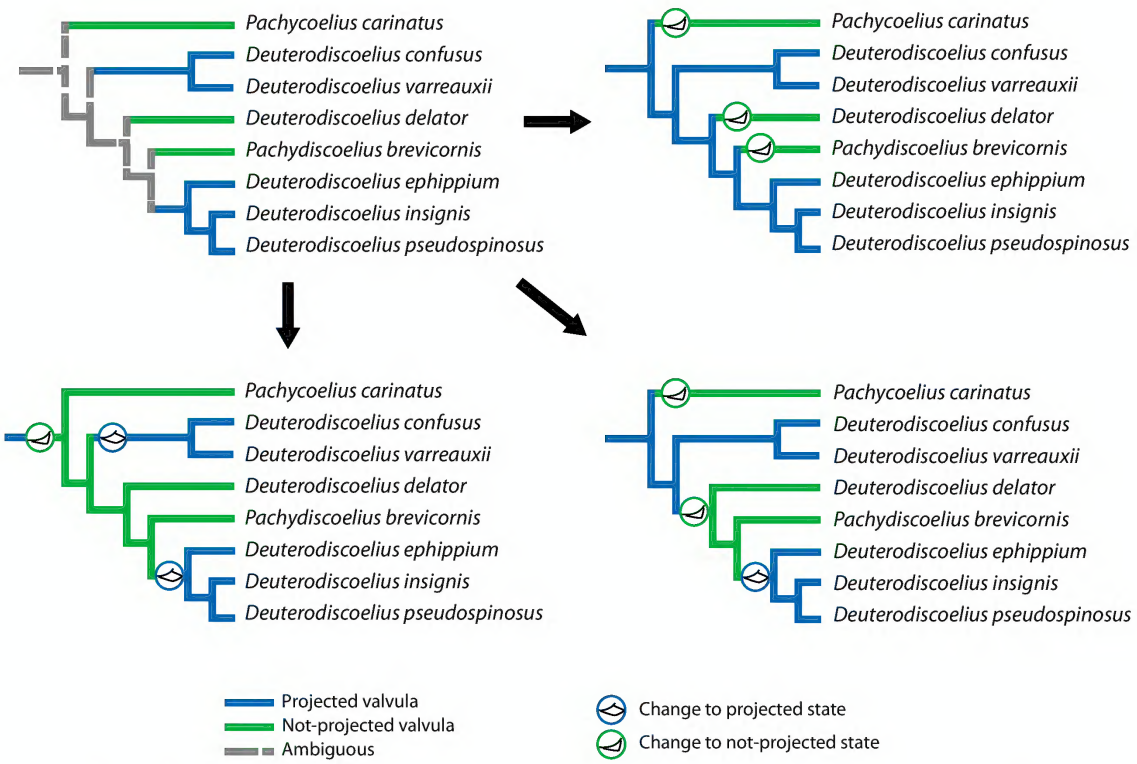

FIGURE 6. Different hypotheses on the state changes of the propodeal valvule. In clockwise order: following a generalized ambiguous scenario (top left): three independent origins of the not-projected state (top right); two independent origins of the not-projected state, one of which is followed by a reversion to the projected state (bottom right); one origin of the not-projected state with two reversions to the projected state (bottom left).

small scrobal spot; subapical bands on T1-2 and S2. Testaceous: femora apically; tibiae and tarsi, except for mid and hind fifth tarsomere; outer two-thirds of tegula.

STRUCTURE: Clypeal apex biconcave. Maxillary palpi very short, shorter than labial palpi. Humeral angles projected. Lowermost region of mesepimeron slightly tumescent. Metanotum strongly bent, with posterior surface flat. Stem of T1 one-third the length of petiole. Expansion of T1 more than 2× as wide as stem and only 1.2× as wide as long. Parategula slender and digitiform. Apical lamellae on T2 and 3 very short, the latter not differentiated form remainder of sclerite. S2 regularly convex. S2–5 with well-developed lamellae. Forewing length: 13.4 mm.

SCULPTURE: Dense macropuntation without micropunctation on clypeus. Very dense micropunctation on frons, eventually coalescent. Vertex with moderate macropunctation and dense micropunctation, except for smooth ocellar region. Pronotal carina lamellar, medially interrupted. Pronotum, mesoscutum, and scutellum densely macro- and micropuntate, presenting only micropuntation surrounding discoid puncture. Notauli present on posterior third. Metanotum very densely macropuntate on dorsal surface, shimmering on posterior surface with microstriae. Propodeum also shimmering, with very dense macropunctures with cariniform interspace, less so medially, with oblique microstriae there. Lateral propodeal carina obsolete. T1 densely macro and micropunctate, with a dorsal longitudinal carina. T2–3 with sparse

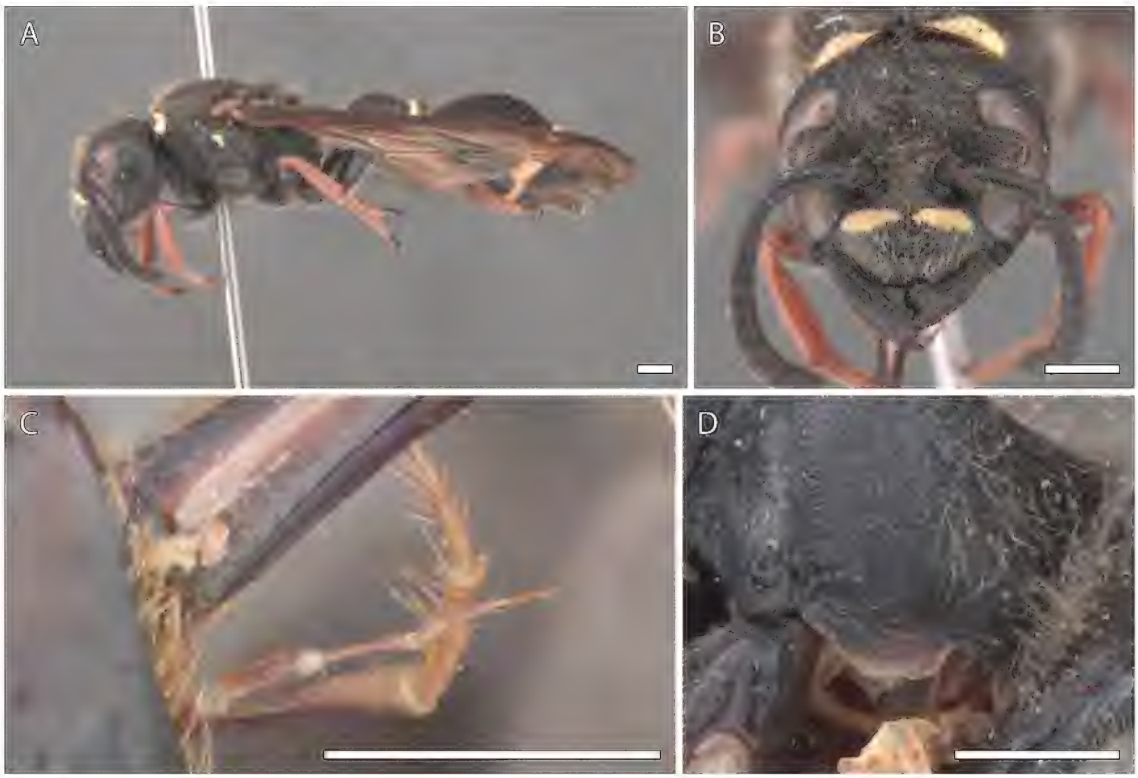

FIGURE 7. *Deuterodiscoelius delator* Lopes and Carpenter, new species. A. Habitus; B. Head, frontal view. C. Maxillary and labial palpi. D. Propodeal valvula. Scales: 1 mm

to moderate macropunctures intercalated by dense micropunctures. T4–6 with dense micropunctures obscuring any macropunctation. S1 smooth with very sparse macropunctures. S2 with sparse to moderate macropunctation, intercalated by smooth areas, except for a completely smooth, impunctate, basal triangle. S3–6 macropunctate with microstriae.

Pilosity: Overall pilosity long and golden. Shorter and sparser on gastral terga, where a dense whitish tomentum prevails.

Male: unknown.

Variations: Forewing length: 11.2–13.4 mm.

Etymology: The specific epithet, from Latin, means "denouncer," or "informer," referring to the fact of bearing traits from two distinct genera, which led to the suspicion of unnatural grouping in these taxa and execution of this study.

Examined material: Holotype: AUSTRALIA: ACT, Blundells/31.i.1970/ E.F. Riek [f#, ANIC]. Paratypes: AUSTRALIA: NSW, Kiandra/ 27.i.1963/ E.F. Riek [f#, ANIC]. CF, Genbrook [f#, ANIC].

CLOSING REMARKS

Our study illustrates how an initially simple idea can expand into greater projects, as we originally aimed to describe an unknown species of zethine Australian wasp. But to do so, we first had to establish the relationship between species of two genera, leading to the synonymy

of *Pachycoelius* under *Deuterodiscoelius*. Finally, this study showcases that significant results in taxonomy and systematics can still be achieved with morphology-exclusive approaches.

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